

**LIFE HISTORY AND DESCRIPTION OF IMMATURE STAGES OF
NEASPILOTA WILSONI BLANC AND FOOTE (DIPTERA: TEPHTRITIDAE) ON
HAZARDIA SQUARROSA (HOOKER AND ARNOTT) E. GREENE
(ASTERACEAE) IN SOUTHERN CALIFORNIA**

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Abstract.—*Neaspilota wilsoni* Blanc and Foote is a univoltine, monophagous fruit fly (Diptera: Tephritidae) developing in the flower heads of *Hazardia squarrosa* (Hooker and Arnott) E. Greene in southern California. The egg, first-, second-, and third-instar larvae, and puparium are described and figured. The egg pedicel is conical and completely circumscribed by many, shallow aeopyles of various sizes. The mouth hooks of all three instars are bidentate. The intersegmental areas of the first instar bear minute acanthae of a heretofore unreported form, i.e., cylindrical and apically bearing one to five prongs. Also newly reported, the caudal segment of the first instar bears stelex sensilla, each basally ringed with one to three, upright, pointed acanthae. The integumental petal is laterally fused with the stomal sense organ in the first instar, but separate in the second instar. The larvae feed mainly on the ovules and soft achenes as first and second instars; however, as third instars, they usually extend their feeding into the receptacle and additionally feed on sap that collects in the shallow scars. The nonfeeding prepuparium overwinters in a protective cell that occupies much of the excavated flower head and is formed of floret, pappus, and achene fragments impregnated with excess sap and liquid feces that harden when dry. A few prepuparia pupariate and emerge as adults in the fall and overwinter, but most pupariate in late winter to early spring, and emerge as adults that aggregate in summer on preblossom host plants to mate and subsequently oviposit. A single male specimen of *Eurytoma veronia* Bugbee (Hymenoptera: Eurytomidae) was reared from a puparium of *N. wilsoni* as a solitary, larval-pupal endoparasitoid.

Key Words: Insecta, *Neaspilota*, *Hazardia*, *Haplopappus*, Asteraceae, nonfrugivorous Tephritidae, biology, taxonomy of immature stages, flower-head feeding, monophagy, seed predation, parasitoids

Revision of the genus *Neaspilota* (Diptera: Tephritidae) by Freidberg and Mathis (1986) facilitated determination of specimens reared from California Asteraceae (Goeden 1989), and stimulated several life-history studies, including one on *N. viridescens* Quisenberry (Goeden and Headrick 1992). This paper de-

scribes the immature stages and life history of a second species from California, *Neaspilota wilsoni* Blanc and Foote.

MATERIALS AND METHODS

The present study was based in large part on dissections of subsamples of flower

heads of *Hazardia squarrosa* (Hooker and Arnott) E. Greene [= *Haplopappus squarrosus* (Hickman 1993)] collected during 1989–1995 from three locations in San Diego Co. in the manner described by Goeden (1985, 1989, 1992): W of Dogpatch along State Hwy. 94 at 760-m elevation; Los Terrenitos N of Interstate Hwy. 8 and junction with State Hwy. 79 at 1,000 m; Kitchen Creek Road above Cibbetts Flat Campground at ca. 1,300 m, Cleveland Nat. Forest. One-liter samples of excised, immature and mature flower heads containing eggs, larvae, and puparia were transported in cold-chests in an air-conditioned vehicle to the laboratory and stored under refrigeration for subsequent dissection, photography, description, and measurement. Six eggs, four first-, three second-, and four third-instar larvae, and three puparia dissected from flower heads were preserved in 70% EtOH for scanning electron microscopy (SEM). Additional puparia were placed in separate, glass shell vials stopped with absorbant cotton and held in humidity chambers at room temperature for adult and parasitoid emergence. Specimens for SEM were hydrated to distilled water in a decreasing series of acidulated EtOH. They were osmicated for 24 h, dehydrated through an increasing series of acidulated EtOH, critically point dried, mounted on stubs, sputter-coated, and studied with a JEOL JSM C-35 SEM in the Department of Nematology, University of California, Riverside.

Most adults reared from isolated puparia were individually caged in 850-ml, clear-plastic, screened-top cages with a cotton wick and basal water reservoir and provisioned with a strip of paper toweling impregnated with yeast hydrolyzate and sucrose. These cages were used for studies of longevity and sexual maturation in the insectary of the Department of Entomology, University of California, Riverside, at $25 \pm 1^\circ\text{C}$, and 14/10 (L/D) photoperiod. Single pairs of virgin males and females obtained from emergence cages also were held in

each of six, clear-plastic, petri dishes provisioned with a flattened, water-moistened pad of absorbant cotton spotted with honey (Headrick and Goeden 1994) for observations of their courtship and copulation behavior.

Plant names used in this paper follow Hickman (1993) and Bremer (1994); tephritid names and adult terminology follow Foote et al. (1993). Terminology and telegraphic format used to describe the immature stages follow Goeden et al. (1998a, b), Goeden and Headrick (1992), Goeden and Teerink (1997; 1998; 1999a, b, c), Teerink and Goeden (1998, 1999), and our earlier works cited therein. Means \pm SE are used throughout this paper. Voucher specimens of *N. wilsoni* adults and immature stages and its parasitoid reside in the research collections of RDG.

RESULTS AND DISCUSSION

Taxonomy

Adult.—*Neaspilota wilsoni* was described by Blanc and Foote (1961) from a male from Jacolitas Canyon, Fresno Co., California. Foote and Blanc (1963) and Foote et al. (1993) pictured the unpatterned wing, as did Freidberg and Mathis (1986) along with drawings of the lateral aspect of the head, male right foretarsus, epandrium and cerci, aculeus and its apex enlarged, and spermatheca.

Immature stages.—The egg, larvae, and puparium heretofore have not been described nor illustrated.

Egg: Twenty-three ova dissected from five, 40+ days-old *N. wilsoni* plus 10 eggs dissected from field-collected flower heads were white, opaque, smooth, elongate-ellipsoidal, 0.93 ± 0.009 (range, 0.82–1.00) mm long, 0.24 ± 0.006 (range, 0.18–0.25) mm wide, smoothly rounded at tapered basal end (Fig. 1A); pedicel conical, 0.02 mm long, completely circumscribed by different sized, mostly circular, shallow aeropyles, through which the spongy inner layers of the chorion are readily visible (Fig. 1B).

The egg of *N. wilsoni* is similar in shape,

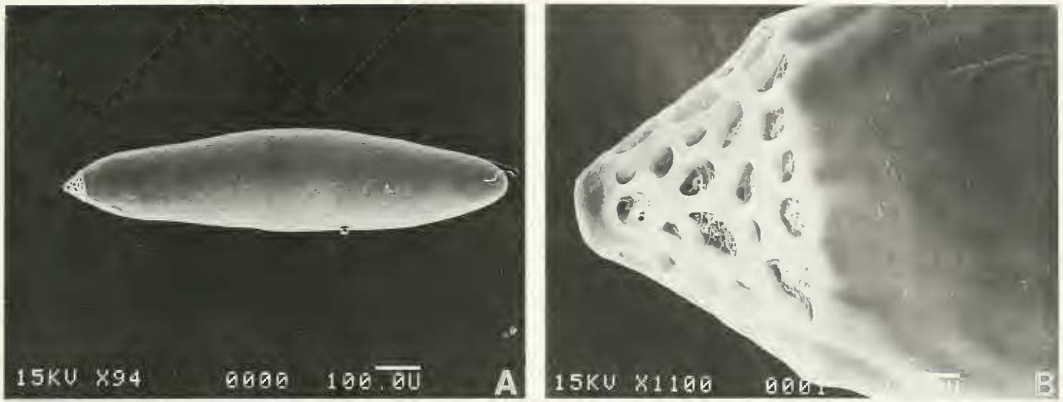


Fig. 1. Egg of *Neaspilota wilsoni*: (A) habitus, anterior end to left; (B) pedicel, aeropyles.

but about 40% longer and 30% wider than that of *N. viridescens* (Goeden and Headrick 1992); moreover, the latter species has fewer aeropyles that are irregularly and less densely spaced around its otherwise similarly-shaped and -sized pedicel. The eggs of 12 species of *Trupanea* from California studied to date, including *T. femoralis* (Thomson), *T. nigricornis* (Coquillett), and *T. wheeleri* Curran that occur in symphagy with *N. wilsoni* in heads of *H. squarrosa* (Goeden 1985, 1992, 1997), have pedicels circumscribed by only one or two rows of aeropyles (Goeden and Teerink 1999b and references therein).

First instar: White, elongate-cylindrical, bluntly rounded anteriorly and posteriorly (not shown); minute acanthae, pointed to cylindrical and apically one- to five-pronged, circumscribe intersegmental lines (Fig. 2A-1, C-1)_s; gnathocephalon smooth, lacking rugose pads, but with pair of prominent integumental petals dorsal to mouthhooks (Fig. 2A-2, B-1); dorsal sensory organ a dome-shaped papilla (Fig. 2A-8, B-2); anterior sensory lobe (Fig. 2A-4, B) bears the terminal sensory organ (Fig. 2A-5, B-3), pit sensory organ (Fig. 2B-4), lateral sensory organ (Fig. 2B-5), and supralateral sensory organ (Fig. 2B-6); stomal sense organ ventrolaterad of anterior sensory lobe (Fig. 2A-6, B-7), integumental petal fused laterally with stomal sense organ (Fig. 2A-6, B-7); mouthhook bidentate

(Fig. 2A-7); median oral lobe laterally flattened, apically pointed (Fig. 2A-8); pit sensillum laterad of dorsal sensory organ (Fig. 2B-8); four verruciform sensilla circumscribe gnathocephalon medially (Fig. 2A-9); metathoracic lateral spiracular complex with a spiracle (Fig. 2C-2) and four, vertically aligned, verruciform sensilla posteriorad (Fig. 2C-3); caudal segment with two stelex sensilla, dorsolaterad and ventrolaterad of posterior spiracular plates, each stelex sensillum basally ringed with one to three, upright, pointed acanthae (Fig. 2D-1); posterior spiracular plate bears two ovoid rimae, ca. 0.006 mm in length (Fig. 2D-2), and four interspiracular processes, each with five to nine branches, longest measuring ca. 0.01 mm (Fig. 2D-3); intermediate sensory complex with one stelex sensillum (Fig. 2D-4).

The first instar is similar in general habitus to that of *N. viridescens* (Goeden and Headrick 1992). However, unlike *N. viridescens*, the dorsal sensory organ of the first instar of *N. wilsoni* is well defined (Fig. 2A-3, B-2), as is the anterior sensory lobe and integumental petal. The reported poor definition of *N. viridescens* may have reflected specimen condition, as the same dissection and preparation procedures as well as scanning electron microscope were used with both species (but see descriptions of later instars below). Also, the pit sensory organ, not visible with *N. viridescens* (Goe-

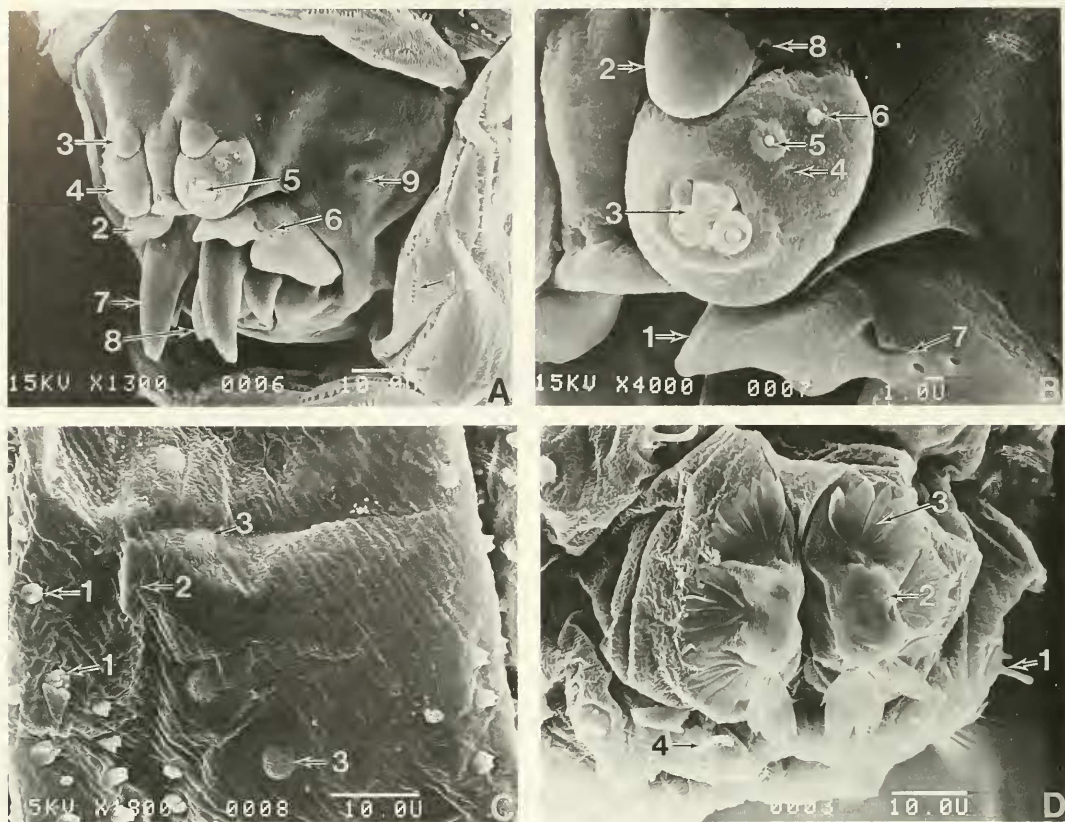


Fig. 2. First instar of *N. wilsoni*: (A) gnathocephalon, gnathocephalon, anterolateral view, 1- minute acanthae, 2- integumental petal, 3- dorsal sensory organ, 4- anterior sensory lobe, 5- terminal sensory organ, 6- stomal sense organ, 7- mouthhook, 8- median oral lobe, 9- campaniform sensillum; (B) anterior sensory lobe, 1- integumental petal, 2- dorsal sensory organ, 3- terminal sensory organ, 4- pit sensory organ, 5- lateral sensory organ, 6- supralateral sensory organ, 7- stomal sense organ, 8- pit sensillum; (C) metathoracic spiracular complex, 1- minute acanthae, 2- spiracle, 3- campaniform sensillum; (D) caudal segment, 1- stelix sensilla, with basal acantha, 2- rima, 3- interspiracular process, 4- intermediate sensory complex, stelix sensillum.

den and Headrick 1992), is clearly seen in *N. wilsoni* (Fig. 2B-4). A fused integumental petal and stomal sense organ also was reported in first instar *Trupanea vicina* (Goeden and Teerink 1999b).

The cylindrical, apically pronged acanthae that circumscribe the intersegmental lines are the first of this type reported from tephritid larvae, as are the lateral stelix sensilla on the caudal segment that are basally ringed with upright, pointed acanthae. The 10 stelix sensilla reported to surround the posterior spiracular plate of the first instar of *N. viridescens* (Goeden and Headrick 1992) are suspect in number. These sensilla

apparently are reduced to four in *N. wilsoni* (Fig. 2D-1, D-4), two sensilla less than the six reported for California *Trupanea* (Goeden and Teerink 1999b and references therein). As another difference, the interspiracular processes of *N. viridescens* have up to four branches (Goeden and Headrick 1992); whereas, *N. wilsoni* possesses up to nine branches (Fig. 2D-3). Needless-to-say, comparative studies of first instars of additional *Neaspilota* spp. are needed to better clarify these contradictory, apparent or real distinctions, which hopefully will be forthcoming in our next several papers.

Second instar: White, elongate-cylindri-

cal, tapering anteriorly, rounded posteriorly (not shown), minute acanthae circumscribe intersegmental lines (Fig. 3A-1, D-1)_s, gnathocephalon conical (Fig. 3A); dorsal sensory organ a dome-shaped papilla (Fig. 3A-2, B-1); anterior sensory lobe (Fig. 3A-3, B) bears the terminal sensory organ (Fig. 3A-4, B-2), lateral sensory organ (Fig. 3B-3), supralateral sensory organ (Fig. 3B-4), and pit sensory organ (Fig. 3B-5); stomal sense organ prominent ventrolaterad of anterior sensory lobe (Fig. 3B-6, C-1); mouthhook bidentate (Fig. 3A-5, C-2); median oral lobe laterally flattened (Fig. 3C-3); two pit sensilla laterad of dorsal sensory organ (Fig. 2B-7); labial lobe with two pore sensilla (Fig. 3C-4); single row of integumental petals dorsal to mouthhook (Fig. 3A-6, B-8, C-5); most oral ridges lateral to mouthhooks dentate along posterior margins (Fig. 3A-7, C-6); pit sensilla circumscribe gnathocephalon medially (Fig. 2A-8); anterior thoracic spiracle with three to four oblong papillae; lateral spiracular complex of mesothorax with a spiracle (Fig. 3D-2) and three verruciform sensilla in vertical row (Fig. 3D-3); caudal segment with at least two stelex sensilla (not shown), dorsolaterad and ventrolaterad of posterior spiracular plates; posterior spiracular plate bears three ovoid rimae, ca. 0.014 mm in length (Fig. 3E-1), and four interspiracular processes, each with two to six branches, longest measuring 0.011 mm (Fig. 3E-2); intermediate sensory complex with a stelex sensillum (Fig. 3F-1) and a medusoid sensillum (Fig. 3F-2).

Few differences were noted between the first and second instars, besides the acquisition of prothoracic spiracles and another rima on the posterior spiracular plate normal to all tephritid larvae (Headrick and Goeden 1998). The dorsal sensory organ is less well defined in the second instar (Fig. 3A-2, B-1) than in the first instar (Fig. 2A-3, B-2). However, the habitus of the second instar of *N. viridescens* was described as barrel-shaped (Goeden and Headrick 1992); whereas, that of *N. wilsoni*, is elongate cy-

lindrical, like the first instars of both species. Another distinction between the first and second instar of *N. wilsoni* is the presence of seven oral ridges with dentate margins in the latter instar, also pictured and equal to, but unquantified until now (unpublished data), for the second instar of *N. viridescens* (Goeden and Headrick 1992). The stomal sense organs of both species bear three sensory structures, described as conical in *N. viridescens* (Goeden and Headrick 1992), but which appear papilliform in *N. wilsoni* (Fig. 3B-6, C-1). The mouth hooks of the second instar of *N. viridescens* are tridentate (Goeden and Headrick 1992); whereas, those of *N. wilsoni* are bidentate (Fig. 3A-5, C-2). Similar, apparent interspecific differences in dentation were noted among mouth hooks of second instar *Trupanea* spp. (Goeden and Teerink 1999b and references therein). Finally, the stelex sensilla on the caudal segment of the second instar of *N. wilsoni* are not basally ringed by pointed acanthae (Fig. 3F-1), as in the first instar (Fig. 2D-1); the interspiracular processes each bear two to six (Fig. 3E-2), not five to nine branches (Fig. 2D-3), respectively; and the intermediate sensory complex consists of a medusoid and a stelex sensillum (Fig. 3F-1, 2), not just a single stelex sensillum (Fig. 2D-4). In contrast, the interspiracular processes of the second instar of *N. viridescens* were noted to be two-branched at most (Goeden and Headrick 1992). Again, comparative studies of second instars of additional species of *Neaspilota* are needed in order to help distinguish real from apparent, intra- and interspecific differences.

Third instar: Mostly white, with last two or three segments darkened, elongate-cylindrical, tapering anteriorly, posterior spiracular plate on caudal segment flattened and upturned dorsally ca. 60°, minute acanthae circumscribe all intersegmental areas and all abdominal segments except pleura (Fig. 4A, F)_s gnathocephalon conical (Fig. 4B); apparently six oral ridges laterad of mouth lumen, all with serrated margins (Fig. 4B-

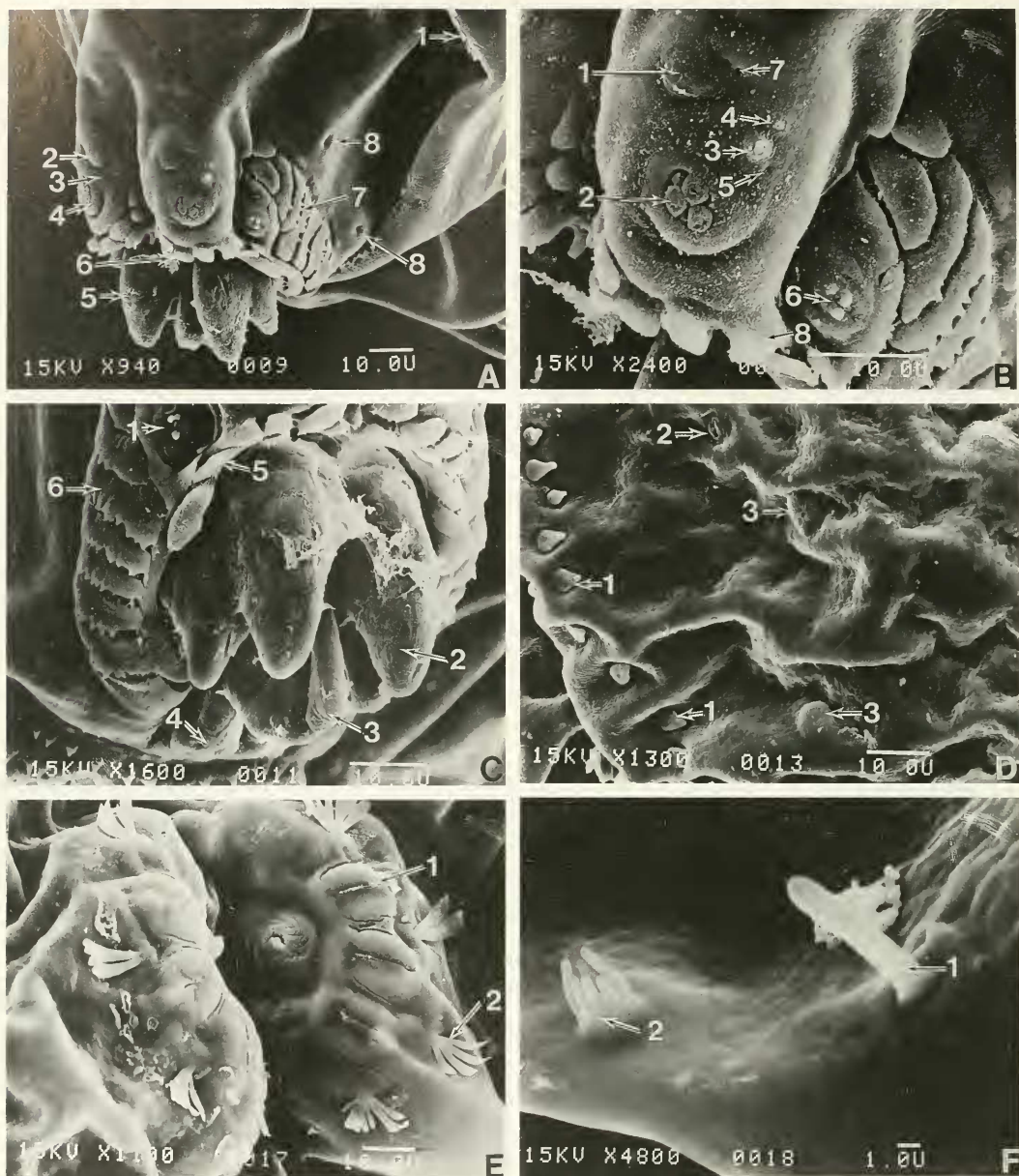


Fig. 3. Second instar of *Neaspilota wilsoni*: (A) gnathocephalon and prothorax, anterolateral view, 1- minute acanthae, 2- dorsal sensory organ, 3- anterior sensory lobe, 4- terminal sensory organ, 5- mouth hook, 6- integumental petal, 7- oral ridge, 8- pit sensilla; (B) anterior sensory lobe, 1- dorsal sensory organ, 2- terminal sense organ, 3- lateral sensory organ, 4- supralateral sensory organ, 5- pit sensory organ, 6- stomal sensory organ, 7- pit sensillum, 8- integumental petal; (C) gnathocephalon, ventrolateral view, 1- stomal sense organ, 2- mouthhook, 3- median oral lobe, 4- labial lobe, 5- integumental petal, 6- oral ridge; (D) metathoracic spiracular complex, 1- minute acanthae, 2- spiracle, 3- campaniform sensilla; (E) caudal segment, 1- rima, 2- interspiracular process; (F) intermediate sensory complex, 1- stelex sensillum, 2- medusoid sensillum.

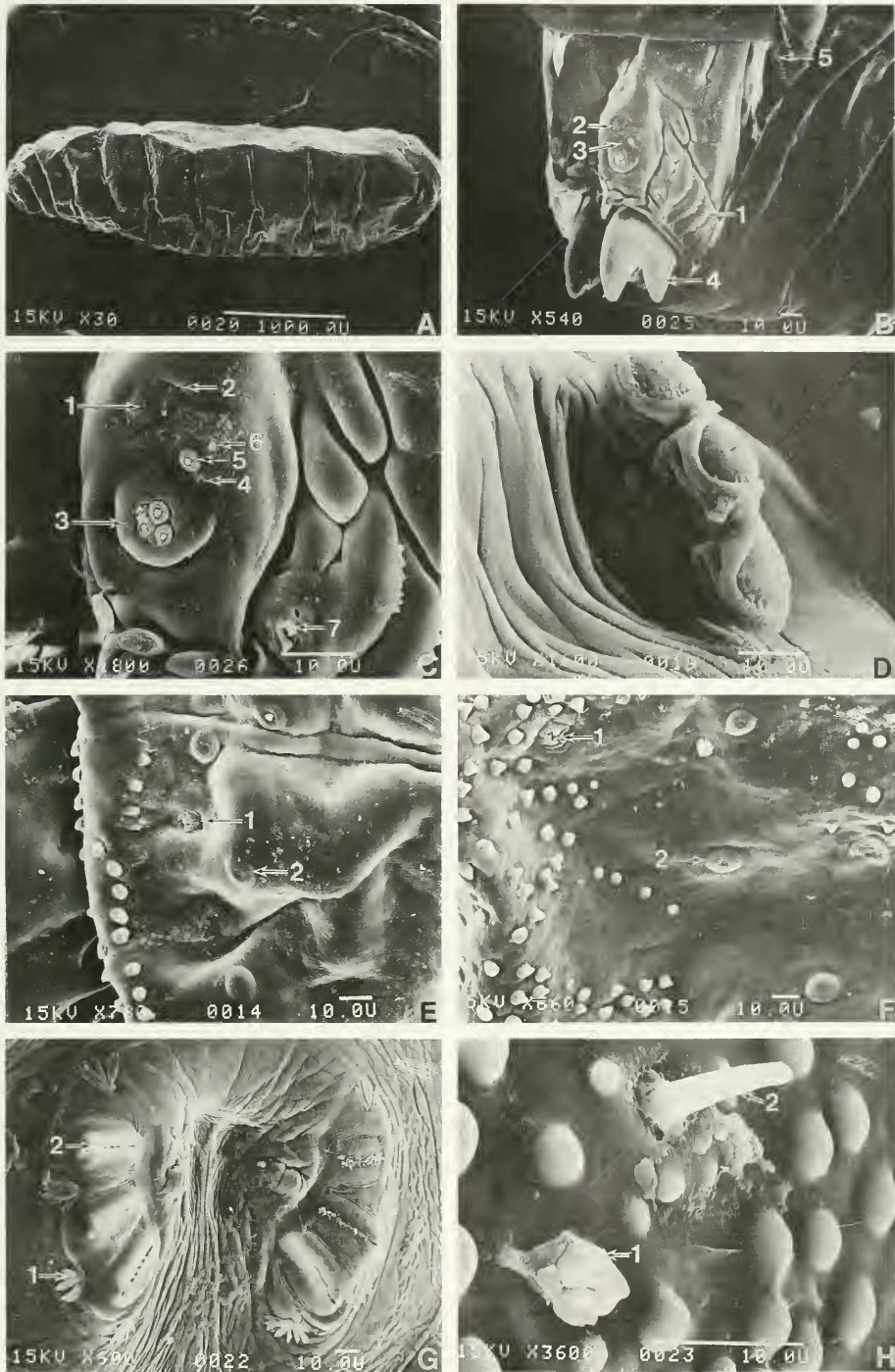


Fig. 4. Third instar of *Neaspilota wilsoni*: (A) habitus, anterior to left; (B) gnathocephalon, anterolateral view, 1- oral ridge, 2- dorsal sensory organ, 3- anterior sensory lobe, 4- mouthhook, 5- minute acanthae; (C) anterior sensory lobe, 1- dorsal sensory organ, 2- pit sensillum, 3- terminal sensory organ, 4- pit sensory organ, 5- lateral sensory organ, 6- supralateral sensory organ, 7- stomal sense organ; (D) anterior thoracic spiracle; (E) metathoracic spiracular complex, 1- spiracle, 2- campaniform sensillum; (F) first abdominal spiracular complex, 1- spiracle, 2- campaniform sensillum; (G) caudal segment, 1- interspiracular process, 2- rima; (H) intermediate sensory complex, 1- medusoid sensillum, 2- stelix sensillum.

1); dorsal sensory organ a dome-shaped papilla (Fig. 4B-2, C-1), pit sensillum laterad of dorsal sensory organ (Fig. 4C-2); anterior sensory lobe (Fig. 4B-3, C) bears the terminal sensory organ (Fig. 4C-3), pit sensory organ (Fig. 4C-4), lateral sensory organ (Fig. 4C-5), and supralateral sensory organ (Fig. 4C-6); stomal sense organ prominent ventrolaterad of anterior sensory lobe (Fig. 4C-7); mouth hook bidentate (Fig. 4B-4); median oral lobe not clearly visible; prothorax circumscribed anteriorly with minute acanthae (Fig. 4B-5); anterior thoracic spiracle bears three oblong papillae (Fig. 4D); metathoracic lateral spiracular complex with a spiracle (Fig. 4E-1) and four verruciform sensilla (Fig. 4E-2); abdominal lateral spiracular complex with a spiracle (Fig. 4F-1), three verruciform sensilla (Fig. 4F-2); caudal segment circumscribed by minute acanthae; stelex sensilla, dorsolaterad, laterad and ventrolaterad of posterior spiracular plate; posterior spiracular plate bears three ovoid rimae, ca. 0.013 mm in length (Fig. 4G-2), and four interspiracular processes (Fig. 4G-1), each with three to four branches each with one to three, apical teeth, longest branch measuring 0.012 mm; intermediate sensory complex with a medusoid (Fig. 4H-1) and a stelex sensillum (Fig. 4H-2).

The habitus of the third instar of *N. wilsoni* generally is like that reported for *N. viridescens* by Goeden and Headrick (1992), except that minute acanthae circumscribe all intersegmental areas and all abdominal segments except the pleura in the former species; whereas, in the latter species the intersegmental areas are free of acanthae. Like the second instar of *N. wilsoni*, the dorsal sensory organ is less well defined in the third instar (Fig. 4B-2, C-1) than in the first instar (Fig. 2A-3, B-2). The dorsal sensory organ in the third instar *N. viridescens* also is not well defined, but this is not a generic character (unpublished data), as proposed by Goeden and Headrick (1992). The stomal sense organs of the third instars of both species bear sensory struc-

tures, described as several cone-shaped sensilla in *N. viridescens* (Goeden and Headrick 1992), but which appear papilliform and pit-type in *N. wilsoni* (Fig. 4C-7). Unlike the second instar of *N. wilsoni*, the third instar apparently has six oral ridges, all with dentate margins, the same as partially pictured, but unquantified, and also now reported for the third instar of *N. viridescens* (Goeden and Headrick 1992 and unpublished data). This may represent a loss from the second instar of one oral ridge in the third instar of both species; however, distinguishing and accurately counting these structures is rendered problematic by degree and angle of exposure of the gnathocephalon as well as by a current lack of a precise definition for and defined morphological limits to these structures (Tesky 1981). The third instars of *Trupanea imperfecta*, *T. jonesi*, *T. nigricornis*, *T. pseudovicina*, *T. signata*, and *T. wheeleri* also bear serrated oral ridges (Goeden and Teerink 1997; 1998, 1999b; Goeden et al. 1998a; Knio et al. 1996a; Teerink and Goeden 1998). Also, like the second instar, the mouthhooks of third instar *N. wilsoni* are bidentate (Fig. 4B-4); whereas, those of *N. viridescens* are tridentate (Goeden and Headrick 1992). Such interspecific differences in dentation are supported by our findings that the mouth hooks of third instar *Trupanea vicina* are bidentate; whereas, those of 12 other congeners examined from California are tridentate (Goeden and Teerink 1999b and citations therein). The abdominal lateral spiracular complex is like that pictured and described for third instar *Stenopa affinis* Quisenberry (Goeden and Headrick 1990).

Puparium: Mostly white to yellow, with posterior two-three segments grayish to blackened posteriorly, broadly ellipsoidal and smoothly rounded at both ends, minute acanthae circumscribe intersegmental lines; anterior end bears the invagination scar (Fig. 5A-1) and anterior thoracic spiracles (Fig. 5A-2); caudal segment circumscribed by minute acanthae (Fig. 5B-1), two stelex

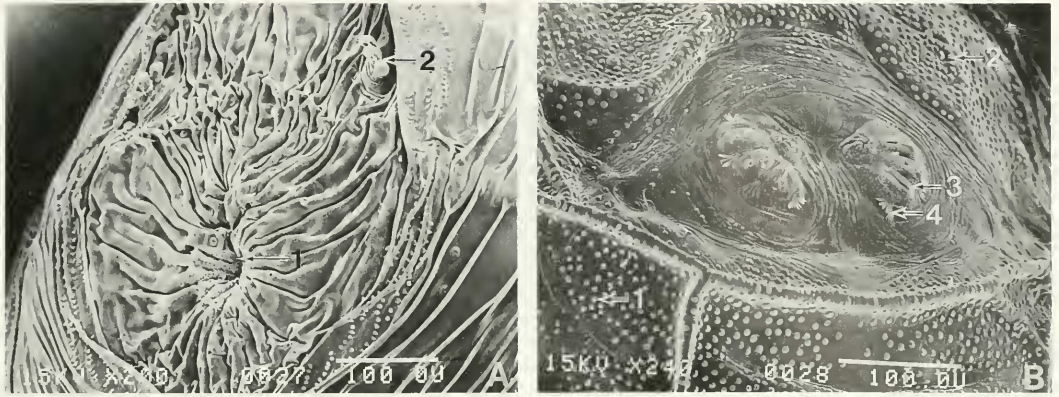


Fig. 5. Puparium of *Neaspilota wilsoni*: (A) anterior end, 1- invagination scar, 2- anterior thoracic spiracle, (B) caudal segment, 1- minute acanthae, 2- stelix sensillum, 3- rima, 4- interspiracular process.

sensilla, dorsad and ventrad of posterior spiracular plates (Fig. 5B-2); posterior spiracular plate bears three broadly elliptical rimae (Fig. 5B-3), and four interspiracular processes, each with 3 to 4 branches (Fig. 5B-4); intermediate sensory complex with a medusoid sensillum and a stelix sensillum. Six puparia averaged 2.75 ± 0.16 (range, 1.99-3.11) mm in length; 1.24 ± 0.03 (range, 1.12-1.32) mm in width.

DISTRIBUTION AND HOSTS

The distribution of *N. wilsoni* as mapped by Foote et al. (1993) restricted this tephritid to California in the United States north of Mexico. The distribution of this true monophage probably also extends southward into northern Baja California like that of its only known host plant, *H. squarrosa* (Freidberg and Mathis 1986, Goeden 1989, Foote et al. 1993), commonly known as "saw-toothed goldenbush" (Hickman 1993), which belongs to the subtribe Solidagininae in the tribe Astereae (Bremer 1994). We here reiterate our belief (Goeden 1989) reported by Foote et al. (1993) that the unconfirmed record for *Coreopsis calliopsidea* Gray in Freidberg and Mathis (1986), which they suspected was a host, probably is not valid, owing to its distant relationship to *Hazardia*; it belongs to the tribe Heliantheae, subtribe Coreopsidinae (Bremer 1994). Furthermore, neither *N. wil-*

soni, nor any other species of *Neaspilota*, has ever been reared from the genus *Coreopsis* in California (Goeden 1989), even during intensive and extensive field study of two principal associates of *Coreopsis* spp., *Dioxyna picciola* (Bigot) (Headrick et al. 1996) and *Trupanea jonesi* Curran (Goeden et al. 1998a).

BIOLOGY

Egg.—In 17 closed, preblossom, apical or penultimate, immature flower heads of *H. squarrosa*, 19 eggs were inserted between or through the phyllaries, usually into or between the inner phyllaries, and perpendicular or at a slight angle (ca. 15°) to the receptacle (Fig. 6A). All eggs were oviposited pedicel-last. Only one flower head contained a floret damaged by oviposition. The diameters of the receptacles of 17 flower heads containing eggs averaged 1.8 ± 0.2 (range, 0.85–3.75) mm, and these heads contained an average of 1.1 ± 0.1 (range, 1–2) eggs.

Larva.—Upon eclosion, first instars tunneled through an inner phyllary into the apical end of an ovule. An average of 1.3 ± 0.2 (range, 1–3) first instars was found feeding within each of 10, closed, preblossom flower heads, the receptacles of which averaged 1.6 ± 0.2 (range, 1.1–2.0) mm in diameter. These infested heads contained an average of 17 ± 1 (range, 15–18) ovules,

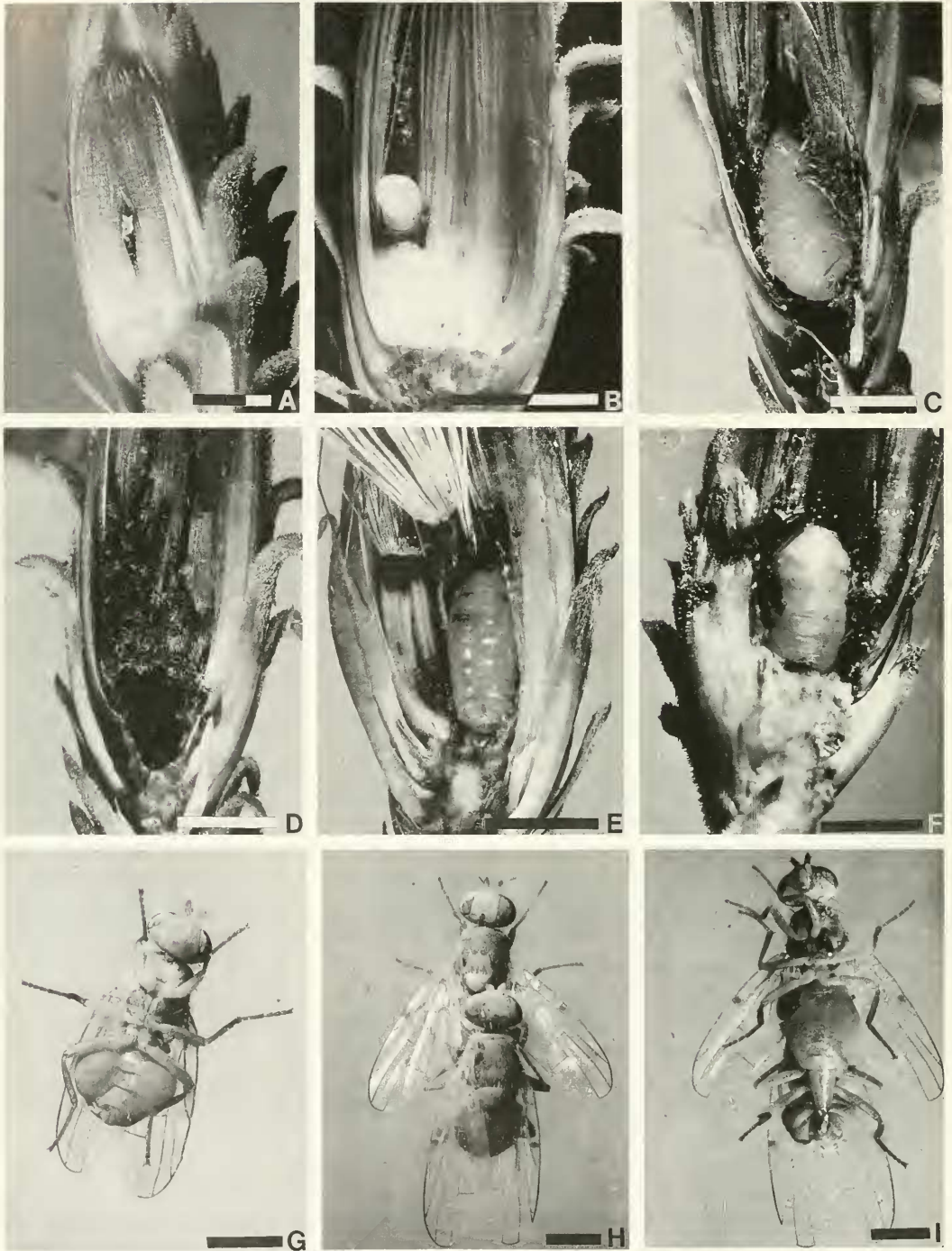


Fig. 6. Life stages of *Neaspilota wilsoni*: (A) egg laid in immature flower head of *Hazardia squarrosa*, (B) second instar feeding on soft achene in open flower head, (C) third instar feeding among soft achenes in center of open flower head, (D) partially opened cell in flower head, (E) prepuparium in flower head, (F) puparium in flower head, (G) male with expanded abdominal pleura, ventral view, (H) mating pair, dorsal view; (I) mating pair, ventral view. Lines = 1 mm.

of which only one or two, or about 8% (range, 6–13%), were damaged. First instars continued to feed on the ovules, most with their mouthparts directed towards the receptacles. No receptacles within these 10 infested flower heads were abraded or pitted by first instar feeding.

Second instars fed mainly in ovules of preblossom flower heads or in soft achenes of open heads (Fig. 6B). About half fed with their bodies perpendicular to and their mouthparts directed towards the receptacles; the others fed horizontal to the receptacles within adjacent ovules/soft achenes, but still well above the receptacles (Fig. 6B). Receptacles of eight flower heads containing second instars were undamaged and averaged 1.7 ± 0.1 (range, 1.4–2.0) mm in diameter. These flower heads each contained a single second instar that had destroyed an average of 4.5 ± 1.2 (range, 1–12) ovules/soft achenes, or about 26% (range, 5–46%) of an average total of 15 ± 1.6 (range, 11–22) ovules/soft achenes.

Third instars fed mainly on ovules or soft achenes in the centers of closed or post-blossom flower heads, respectively (Fig. 6C). In 24 flower heads averaging 1.8 ± 0.6 (range, 1.4–2.3) mm in diameter and containing an average of 1.0 ± 0.04 (range, 1–2) third instars, from eight to all of the ovules/soft achenes therein were damaged, or about 60 to 100% of an average total of 14 soft achenes per head contained in a separate subsample of 47 uninfested, mature flower heads. Third instars in flower heads fed with their long axes oriented perpendicular to and mouthparts directed towards the receptacles (Fig. 6C). Two-thirds of the third instars in the 24 infested heads scored or pitted the receptacles, or used the basal stumps of achenes as conduits, and thus supplemented their diet with sap. Goeden and Headrick (1992) described and discussed this similar type of feeding by *N. viridescens*. And, as they also reported for *N. viridescens*, the third instar became surrounded for about 90% its length by a cell, which occupied most of the interior of the

flower head and consisted of ovule-, achene-, pappus-, and floral tube-fragments cemented together by liquid feces and sap that hardened when dry (Fig. 6D). These protective cells externally incorporated the outer walls of achenes and the few uneaten achenes, were blackened and smooth inside, and averaged 2.4 ± 1.4 (range, 1.0–3.8) mm long by 1.8 ± 0.4 (range, 0.8–2.6) mm wide and about 0.2 mm in wall thickness (Fig. 6D). Upon completing their feeding and cell construction, the larvae oriented with their anterior ends away from the receptacles, retracted their mouthparts, and formed prepuparia (Headrick and Goeden 1998). Most individuals overwintered in diapause as prepuparia (Fig. 6E) (Goeden and Headrick 1992, Headrick and Goeden 1998), but <10% pupariated (Fig. 6F).

Pupa.—Puparia (Fig. 6F) formed in flower heads in the fall produced adults that emerged by pushing aside the loose plug of excised pappus bristles and other debris at the cell apex. A portion of those few adults that emerged earliest possibly matured, mated, and produced a small partial second generation on late-formed flowerheads, while the few other adults that emerged later probably remained sexually immature and overwintered, like some other monophagous, aggregative tephritids, to reproduce when their hosts again flowered (Headrick and Goeden 1994, 1998).

Adult.—Adults emerged from mature flower heads, and were long-lived under insectary conditions, as 14 unmated males averaged 66 ± 13 (range, 11–147) days, and 13 virgin females averaged 92 ± 15 (range, 19–171) days. Such lengthy longevities are commensurate with the aggregative type of life cycle described below for this tephritid, and compare favorably with average adult longevities of 87 and 86 days, respectively, reported for male and female *N. viridescens* (Goeden and Headrick 1992).

The pre-mating and mating behaviors of *N. wilsoni* were not studied in the field, but were observed in petri dish arenas found to be so useful with many other noncongener-

ic, nonfrugivorous, tephritid species (Headrick and Goeden 1994), including *N. viridescens* (Goeden and Headrick 1992). Premating behaviors observed with *N. wilsoni* were abdominal pleural distension (Fig. 6G), side-stepping, and swaying by males (Headrick and Goeden 1994), and wing hama-tion by both sexes (Headrick and Goeden 1994). However, no trophallaxis or nuptial gift presentation was noted as reported with *N. viridescens* (Goeden and Headrick 1992). Four matings were observed during the early afternoon with different pairs of flies of 255-, 175-, 145-, 140-min duration and one late-morning mating that lasted 235 min; similarly long mating durations were reported with *N. viridescens* by Goeden and Headrick (1992). Disengagement, rarely observed in *Neaspilota* spp. (Headrick and Goeden 1994), was seen once and involved a male turning 180° as he rapidly dismounted and walked away from the female while pulling free his genitalia, as reported with other genera (Headrick and Goeden 1994, Goeden and Teerink 1999b). No post-copulatory behavior was observed other than individual groomings by both flies, and the male storing his genitalia.

Seasonal history.—The life cycle of *N. wilsoni* in southern California follows an aggregative pattern (Headrick and Goeden 1994, 1998) in which the long-lived prepuparia are the principal overwintering stage contained in cells in dead flower heads that remain attached to plants. Come late winter to early spring (February–April), following pupation, the adults emerge and join the few surviving overwintered adults to aggregate in summer (June–August) on long-flowering *H. squarrosa* for mating and oviposition to complete the life cycle. As noted above, a small partial second generation may be produced, although *N. wilsoni* principally is a univoltine species.

Natural enemies.—A single male specimen of *Eurytoma veronia* Bugbee (Hymenoptera: Eurytomidae) was reared from a

puparium of *N. wilsoni* as a solitary, larval-pupal endoparasitoid.

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